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Examensarbete i ämnet biologi
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Abstract

The three-toed woodpecker (*Picoides tridactylus* L.) is a forest specialist bird, highly dependent on dead and decaying trees for foraging. I investigated the occurrence of the three-toed woodpecker in relation to vegetation characteristics including dead wood in the boreal forests of northern Sweden. Forty old forest stands were studied, were I collected data on living and dead trees, and related them to the occurrence of the three-toed woodpecker during the breeding season. Logistic regression was used to model the occurrence of the three-toed woodpecker in relation to habitat variables. I found that of all variables taken in consideration, the amount of freshly dead Norway spruce (*Picea abies* L.) contributed most to explaining the occurrence of three-toed woodpecker. The probability to find three-toed woodpecker in a stand increased with the basal area of freshly dead spruce, the size of the stand, the basal area of living deciduous trees and that of dying Scots pines. A probability of occurrence of 0.5 corresponded to 1.8 m^2/ha of freshly dead spruce. The results refined the knowledge about three-toed woodpecker requirements, underlying the importance of spruce for foraging, and adding information on which decay stage is more preferable for the species. Taking in consideration the fact that the species is declining and included in the Swedish Red List, this study will help defining future targets for conservation management for the three-toed woodpecker.

Key Words: three-toed woodpecker, dead wood, dead spruce, snags, habitat requirements, boreal forest, forest management

1. Introduction

A long history of forest utilization has led to profound changes in boreal forest ecosystems; this has resulted in losses of biodiversity and a decrease in habitat quality for large numbers of specialized species (Berg et al. 1994, Siitonen 2001). The introduction of even-aged stands regenerated after clear felling has led to a decrease in large-diameter trees, dead and decaying wood, deciduous trees and natural disturbances (Johansson et al. 2013). Natural disturbances like forest fire and windthrow are important factors contributing to structural complexity in natural boreal forest systems (Angelstam and Kuuluvainen 2004).

Several resident forest bird species in Fennoscandia which are associated with old successional stages have declined due to loss of old-growth forest stands (Angelstam and Mikusinski 1994) and dead wood in managed forests (Jonsson et al. 2005). Woodpecker populations in Fennoscandia have suffered considerably due to these changes. Woodpeckers are considered as one of the most demanding guild in terms of ecological requirements (Bütler et al. 2004a). Some woodpecker species require large areas with old forest for foraging and breeding (Angelstam and Mikusinski 1994), and their nests are often excavated in old deciduous trees. Moreover, some woodpeckers are considered as umbrella species for the conservation of other species dependent on similar habitats (Martikainen et al. 1998, Roberge et al. 2008).

In boreal coniferous-dominated forests, the three-toed woodpecker (*Picoides tridactylus* L.) is considered a habitat specialist. As a primary hole nester, it provides breeding opportunities for many other species (Pechacek 1995). Besides, it is considered as an important indicator of species-rich bird assemblages in coniferous-dominated natural forests (Roberge and Angelstam 2006) and Romero-Calcerrada and Luque (2006) considered this species as a good indicator for temporal and spatial landscape changes. The three-toed woodpecker occurs in mature boreal to montane coniferous forests, often mixed with deciduous tree species; its distribution follows that of the spruce *Picea* spp. (Baldwin 1968, Bock and Bock 1974).

The three-toed woodpecker is resident with some irregular movements usually in autumn, and Swedish populations are mostly sedentary (Svensson et al. 1999). In the boreal zone, three-toed woodpeckers are important predators of insects that colonize dying and recently dead trees (Bütler et al. 2004a). Although they are considered beetle specialists (Coulson and Witter 1984), the dietary preferences of the species change seasonally. In winter they feed almost exclusively on bark beetles (Curculionidae: Scolytinae), with a marked preference for the species that colonize spruce, e.g. Ips and Polygraphus spp., *Crypturgus subcribrosus* E., *Pityogenes chalcographus* L. (Fayt 1999). In contrast, during the summer they feed largely on wood-boring beetle larvae, in particular on longhorn beetle (Cerambycidae) (Hogstad 1970, Pechacek and Kristin 2004). They forage in stands with

different composition of decayed trees (Hogstad 1970, Wesołowski and Tomialojc 1986, Fayt 2003). Three-toed woodpeckers have the ability to concentrate locally in burned forest or windfall areas, which occasionally produce large amount of dead wood which is rapidly colonized by its prey insects (Koplin 1969, Murphy and Lehnhausen 1998).

There is a clear conflict between three-toed woodpecker habitat and commercial forestry, where it is common practice to remove old, large trees and dead wood from forests. It has been found that the recent decline in the Fennoscandian three-toed woodpecker population is directly related to this type of forest management (Nilsson et al. 1992, Angelstam and Mikusinski 1994, Tucker and Heath 1994). A negative trend has been observed in many breeding populations of northern Europe during the past decades (Pakkala et al. 2002). The loss of suitable habitat and decrease in habitat quality indicate problems for the persistence of viable populations in modern managed forest landscapes (Bütler et al. 2004a). Three-toed woodpecker is currently classified as near-threatened on the Swedish Red List (Gärdenfors et al. 2015).

Dead wood has been identified as one of the most important ecological factors for the conservation of forest biodiversity (Stokland et al. 2004). The amount of dead wood is considered as an essential characteristic of natural forests and has been proposed as indicator of forest naturalness (Siitonen 2001, Simila et al. 2006). Dead wood is used as a quantitative indicator of biodiversity in the reports of the Ministerial Conference on the Protection of Forests in Europe (MCPFE) since 2003 (http://www.foresteurope.org/). Decaying wood provides important habitat for a large number of species (Humphrey and Bailey 2012), and woodpeckers are among the most demanding species connected to dead and dying wood (Mikusinski and Angelstam 1997). The three-toed woodpecker is directly linked with dead wood (Bütler et al. 2004b) and different authors have searched for quantitative targets for its dead wood requirements. Bütler et al. (2004b) investigated the importance of dying and dead standing trees (snags) in relation to the presence and absence of tree-toed woodpeckers. They found a threshold of almost 1.6 m²/ha (basal area) of standing dead wood with a dbh > 10 cm, within an area with a size of an average home-range (44-176 ha). In a study by Bütler et al. (2004a) a comparison was made between forest of south-central Sweden and Switzerland. They found that the probability of three-toed woodpecker occurrence increased from 0.10 to 0.95 when snag basal area increased from 0.6 to 1.3 m²/ha in Switzerland in contrast to 0.3 to 0.5 m²/ha in Sweden (Angelstam et al. 2003). Roberge et al. (2008) also found that the presence of the three-toed woodpecker was positively linked to the basal area of coniferous snags. By basal areas of coniferous snags of 1.0 m²/ha in south-central Sweden and 2.9 m²/ha in northeastern Poland, the tree-toed woodpecker had a probability of 0.9 to occur. Also in Poland, Czeszczewik et al. (2013) found that it would be best to leave at least 2 m²/ha (basal area) of freshly killed spruce after each bark beetle outbreaks.

Despite the recognized importance of dead wood for the three-toed woodpecker (Amcoff and Eriksson 1996, Wesołowski et al. 2005), past studies have mostly focused on coarse measures of dead wood, e.g. the amount of coniferous snags (i.e. standing dead trees (Roberge et al. 2008)). In contrast, there is very little knowledge about the requirements of the species in terms of more refined measures including different qualities of standing dead wood.
Decomposition of dead wood is commonly subdivided in different decay stages. This is usually done using a classification system which considers the visual appearance of trees, the softness of the wood and the loss of biomass (Stokland et al. 2012). In addition to decay stages, standing dead trees can differ in terms of tree species, degree of bark coverage, stem diameter, etc.

In this study I investigated the occurrence of three-toed woodpecker in relation to different qualities of dead wood in the boreal forests of northern Sweden. In order to investigate if dead wood quality is potentially important for the three-toed woodpeckers, I took four hypotheses in consideration. I started with a general hypothesis to test if occurrence of the tree-toed woodpecker can be explained by the amount of dead and living conifers and deciduous trees. Thereafter, I tested hypotheses involving increasingly refined data about dead wood and dying trees. Specifically, I tested the following hypotheses:

1. Presence of the three-toed woodpecker can be explained by the amounts of dead and living conifers and deciduous trees:

> It is well known that the three-toed woodpecker prefers coniferous-dominated natural forests (Angelstam and Mikusinski 1994, Pechacek and d'Oleire-Oltmanns 2004) and its occurrence has been linked to the availability of coniferous snags (Roberge et al. 2008). However, according to Wesołowski and Tomialojc (1986), the three-toed woodpecker can also breed in forests with large proportions of deciduous trees. Therefore, data about both coniferous and deciduous trees may potentially be useful for predicting occurrence of the species.

2. Distinguishing between Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.) increases our ability to model the presence of the three-toed woodpecker, compared to considering both conifers together in one pooled variable:

> Many previous studies suggest that spruce could be more important than other tree species as a foraging substrate (Bütler et al. 2004b, Fayt 2004, Pechacek and d'Oleire-Oltmanns 2004). It may therefore be important to consider separately the

two main native conifer species occurring in Sweden.

3. Distinguishing between dying and healthy living trees increases our ability to model the presence of the three-toed woodpecker, compared to coarser data considering all living trees of each tree species in one pooled variable:

> The requirements of the three-toed woodpecker in terms of dead trees have been largely emphasized (Derleth et al. 2000, Bütler et al. 2004b, Roberge et al. 2008, Czeszczewik et al. 2013). However, there are indications that it also uses dying trees for feeding (Hogstad 1970, Pakkala et al. 2002, Wesołowski et al. 2005).

4. Refining data about the qualities of snags beyond tree species (in terms of decay stages, bark cover and stem diameter) increases our ability to model the presence of the three-toed woodpecker, compared to considering all types of snags in one category:

> It is widely recognized that snags are important for the species, but to my knowledge, no habitat studies about the three-toed woodpecker have split snags into different categories. It can be hypothesized that snags of different qualities provide different amounts of food for the woodpecker in terms of saproxylic beetles. Hence snags of some specific qualities would make a more important contribution to habitat quality than other types of snags.

2. Materials and Methods

2.1 Study Area

The study area is situated in the middle boreal forest zone in the counties of Västernorrland and Västerbotten in northern Sweden (Figure 1). The study design includes 40 mature to old forest stands. The study stands were all selected to initially be as similar as possible in terms of age (mature or overmature stands), productivity and tree species composition. All stands are conifer-dominated, with mixtures of Scots pine and Norway spruce and at least 10% of deciduous trees. The most common deciduous tree species are silver birch (*Betula pendula* R.), downy birch (*Betula pubescens* E.), European aspen (*Populus tremula* L.), grey alder (*Alnus incana* L.), willows (*Salix* sp.) and rowans (*Sorbus aucuparia* L.).

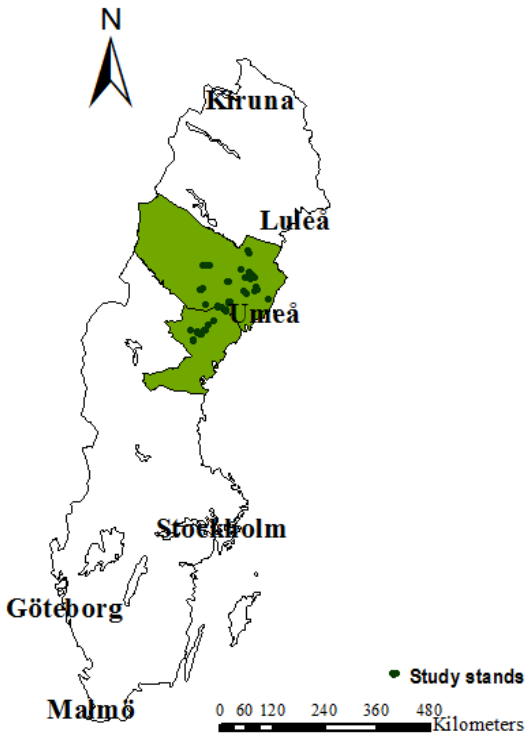


Figure 1- Map of Sweden with the location of the study sites. The study stands are shown as green dots and the counties of Västernorrland and Västerbotten are shown in light green.

The size of the stands ranges from 3 to 22 ha and neighboring study stands are separated from each other by ≥500 m. Moreover, they are representative of different management histories. Ten stands are part of formal nature reserves in which no recent management has taken place and the degree of naturalness is very high. The remaining 30 stands are voluntary forest set-asides, areas of particular conservation interest which are dedicated to

biodiversity conservation (Bernes et al. 2014). Most of these set-asides currently have limited conservation value due to past industrial management. Ten set-aside stands are unmanaged control areas, ten were subjected to ecological restoration through gap cutting and ten were subjected to prescribed burning (Figure 2). These restoration treatments (gap cutting and prescribed burning) were implemented in 2011. Canopy gap-cuttings involved the creation of small clearings of 20 m diameter around a central tree; there are six gaps per ha and they cover on average 19% of the stands. Dead wood was artificially created and left on spot in 50% of the gaps while in the other 50% of the gaps all trees were removed. This resulted in the creation of approximately 10 m^3/ha of fresh dead coniferous and 1-5 m^3/ha of deciduous dead wood. Prescribed burning involved burning preceded by partial thinning of about 5-30% of Norway spruce. Five m^3/ha of cut coniferous trees were left in each stand prior to burning.

Figure 2 (a, b, c, d)- From the upper left: an unmanaged control set-aside, a burning, a gap cutting and a nature reserve.

2.2 Three-toed woodpecker surveys

Data on three-toed woodpecker presence was collected during the breeding season of 2015. From the first of April to the end of June, all stands were visited six times using the territory mapping method (Bibby et al. 1992). During each visit, all individuals showing territorial behaviour were recorded. The surveys were conducted by two experienced ornithologists. A fixed path (parallel lines separated by 80 m) was used to cover the whole

stand area plus a 50-m buffer around it. The exact position of each observed three-toed woodpecker was registered using a Global Positioning System (GPS). Surveys started one half-hour before sunrise and lasted until seven hours after. However, in June starting time was fixed at 02:30 am. Each stand was revisited at intervals of six to ten days. An observer surveyed two stands in a single morning. Considering that the time of day may influence bird activity, the ordering of stand within mornings was shifted between visits. No surveys were performed under heavy rain or strong winds.

2.3 Forest measurements

Stand characteristics were measured in sampling plots systematically distributed within the stands. Due to differences in the sizes of study stands, the number of sampling plots was based on stand size: one sampling plot per 1.5 ha was used, resulting in a total of 250 plots. Plots were located at least 40 m from the edge of the study stand and the distance between sampling plots was ≥80 m.

Measurements consisted in recording diameter at breast height (dbh) for all trees species and performing additional measurements (decay, bark coverage) for snags. The minimal dbh for recorded trees was 5 cm, and the minimal height for broken snags was 1.3 m. Snag decay stages were defined according to Keen (1955) and Thomas et al. (1979). The process of deterioration and decay is divided in seven stages, hereafter ´decay classes´: Class 1 is for living trees, Class 2 for dying and declining trees which are still alive, Class 3 for dead trees with bark, Class 4 for dead trees with losses of bark, Class 5 for completely debarked trees, Class 6 for broken and debarked trees, Class 7 for decomposed trees (Figure 3). Indicators used to define decay stage 2 were: crown damage following the parameters of the Kronutglesning of the Swedish National Forest Inventory (http://www.slu.se/en/collaborative-centres-and-projects/swedish-national-forest-inventory/) and the presence of red needles. These trees (decay class 2) are considered as “dying trees” in my analyses. For trees in decay class 4, the extent of bark loss was recorded to the nearest 10%.

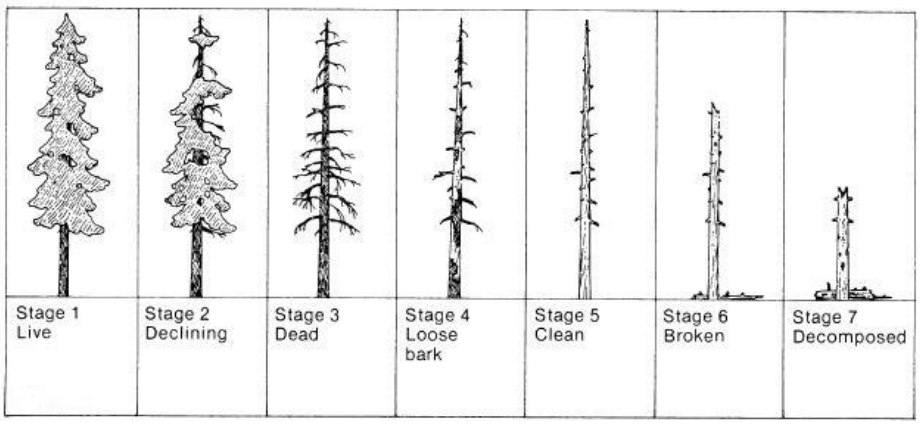


Figure 3- Classes of decay of a snag (Thomas et al. 1979)

All conifer trees belonging to decay class 1 (i.e. healthy living trees) were recorded within a radius of 10 meter from the middle of the sampling plot. Other tree types are usually rarer than healthy conifers and hence require larger sampling plots. Therefore, trees of all other decay classes for conifers and all decay classes of deciduous trees were recorded within a radius of 35 m.

2.4 Data analysis

I used statistical models to analyze the habitat requirements of the three-toed woodpecker, based on presence/absence data. For the purpose of this study, I considered the woodpecker to be "present" when an individual was observed at least twice across the six surveys in a given stand. This approach was used to increase the level of certainty that the stand was actually part of the core breeding territory of the woodpecker. Hence, this threshold (≥2 visits with observed woodpecker) provides a more conservative breeding index than using a single observation threshold.

All statistical analyses were performed at the scale of forest stands (n=40). For that purpose, I computed the mean values for the different forest vegetation variables across plots in each stand to get one single mean value per stand for each variable. For the stands with presence of the woodpecker, only the forest vegetation plots located in the vicinity of the actual sighting locations were used for calculating the stand mean. This was done to avoid including forest data from parts of the stands which may not have been used by the woodpeckers. Hence, if a woodpecker was observed in one part of a very large forest stand with some variation in forest structure, the forest data used in the analyses reflected the part of the stand actually used by the bird. For that purpose, I created a buffer of 200 m radius around each sighting location in a geographic information system (ArcGIS). In further analyses, only the plots located within these buffers were included for calculation of the stand-wise means in stands with presence of the woodpecker. For stands where the

woodpecker was absent, all vegetation sampling plots were included to calculate the stand-wise means.

Tree-layer data was converted into basal area by using the dbh of the tree trunk section at breast height. Basal area per sampling plot was summed and translated into mean basal area per ha for each study stand. The focus of this study was on the internal characteristics of the forest habitat. However, considering that the three-toed woodpecker has large home ranges, I also included some data about the landscape surrounding of the study stands and stand size in the models (see below) to control for the potential effects of these spatial variables on the occurrence of the woodpecker. It has been stated that three-toed woodpecker prefers old forests, in most cases more than 120 years (Angelstam et al. 2005). In this study I considered old-forest of more than 100 years as potentially suitable habitat for three-toed woodpecker. As landscape variable I took the percentage of old forests in the 1 km buffer around the study stands. This was used in the statistical analysis as a "Local landscape quality" variable. I extracted data on forest age from the k Nearest Neighbours (kNN) database, a raster-based data-set (resolution 25x25 m; reference year 2010) that describes forest land in Sweden (Reese et al. 2002). It is a combination of data from the Swedish National Forest Inventory and satellite data (SLU Forest Map). I also included a variable describing the area of the study stands to control for the differences in stand size.

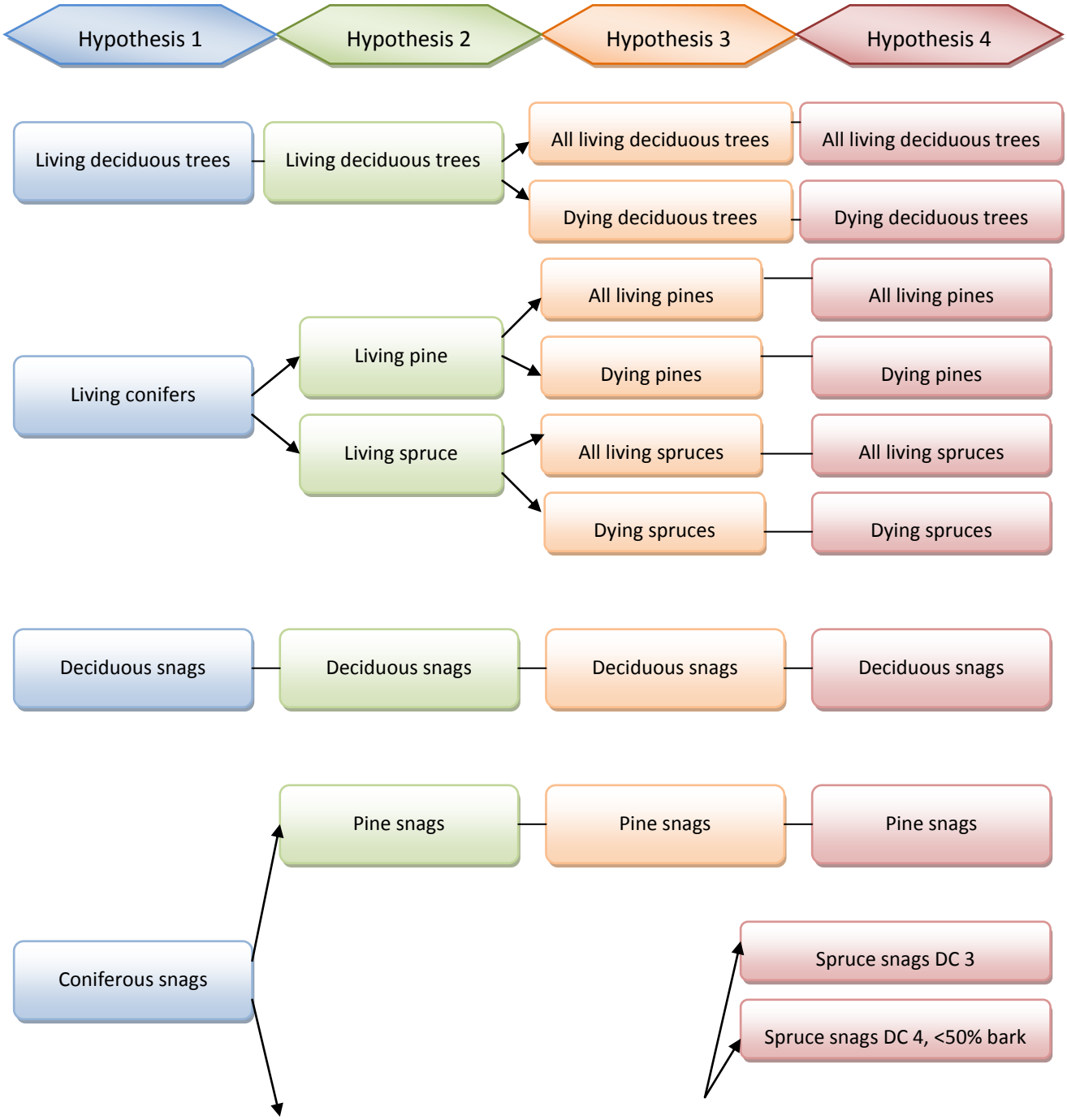
I used Spearman's rank correlation coefficient to test for collinearity among explanatory variables. The correlation coefficients for all possible pair of explanatory variables included in my models were all below the threshold value of 0.7 (Dormann et al. 2013).

I formulated four global models corresponding to the four hypotheses mentioned above (cf. Introduction and Figure 4). These global models represent gradually increasing degrees of refinement (i.e. “thematic resolution”) of the tree-layer data from Hypothesis 1 to Hypothesis 4. In addition to tree-layer variables based on my field measurements, I also included stand area and local landscape quality in all global models to control for potential area and landscape effects. For Hypothesis 4, which addresses snags of different qualities, I focused on refining the snag quality data for spruce only, because previous models (cf. Hypotheses 2 and 3) showed that pine or deciduous snags did not contribute to explaining occurrence of the woodpecker (see Results). The global model included 6 explanatory variables for Hypothesis 1, 8 for Hypothesis 2, 11 for Hypothesis 3 and 15 for Hypothesis 4 (Figure 4).

I used Generalized Linear Models (GLM) with binomial errors and logit link function to test each hypothesis. Starting from the global model for each hypothesis, all possible models (i.e. all possible combinations of explanatory variables) were tested. I used Akaike´s Information Criterion (AIC) to identify the best models. Specifically, I used the second-order Akaike´s Information Criterion (AICc), which is more accurate than AIC when sample size is small (Motulsky and Christopoulos 2003). For each best model I

calculated the p-value of the explanatory variable based on the likelihood ratio test. I also calculated the degree of importance of all variables across all possible models, based on the Akaike weights of the models where they were included. The highest the AICc weight is, the more important is the variable in explaining the response.

For statistical analyses I used the R 3.2.2 software (R Core Team 2015), in particular the 'glmulti' package (Calcagno 2013) for GLM analysis and the 'AICcmodavg' package (Mazerolle M. J. 2015) for AICc calculation.



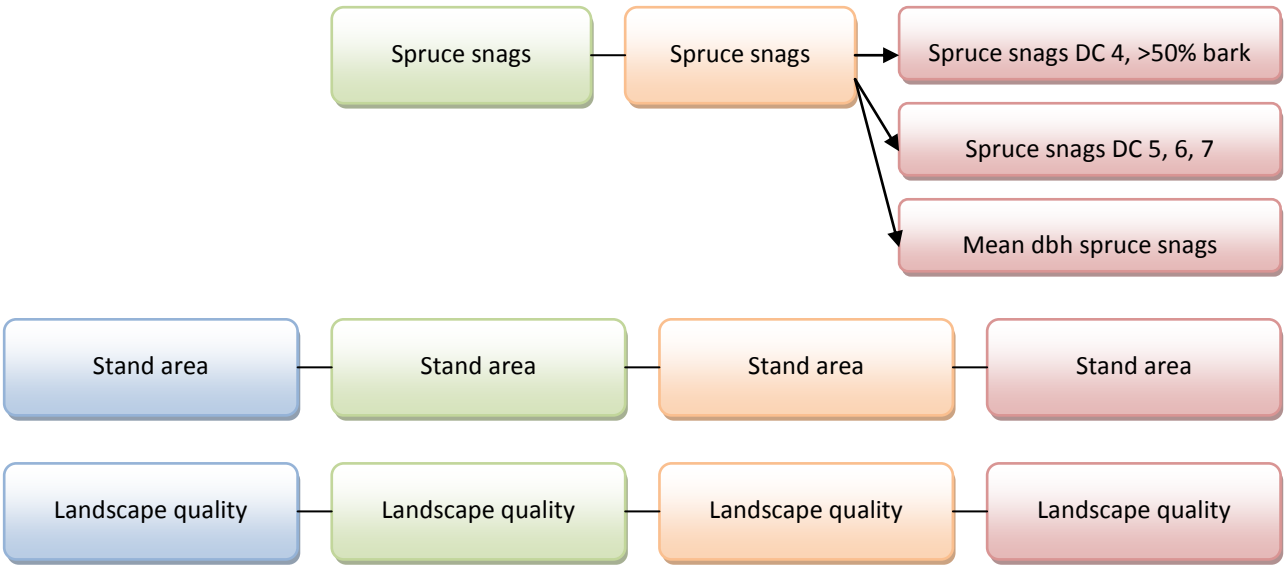


Figure 4- The four hypotheses and their explanatory variables included in the global model addressing each of them. The letters "DC" mean "decay class".

3. Results

The three-toed woodpecker was deemed present (see definition above) in 14 of the 40 study stands (Appendix 1). At the coarsest level of thematic resolution (Hypothesis 1), the best model included three explanatory variables: basal area of coniferous snags, stand area and basal area of living deciduous trees (Table 2). All variables had a positive relation to three-toed woodpecker occurrence. Distinguishing between the two conifer species (Hypothesis 2) slightly improved the ability of the model to predict occurrence of the woodpecker compared to the coarser model developed for Hypothesis 1 (ΔAICc = 1.8). The best model for Hypothesis 2 contained the same variables as for Hypothesis 1, except that the basal area of coniferous snags was replaced by that of spruce snags (Table 2).
Adding specific data about dying trees (Hypothesis 3) improved the model only very slightly compared to the model developed for Hypothesis 2 (ΔAICc = 0.5). Here, the best model contained the same variables as that for Hypothesis 2, plus the basal area of dying pines (positive sign; Table 2). Distinguishing between different decay stages of the spruce snags (cf. Hypothesis 4) considerably improved the ability of the model to predict three-toed woodpecker's occurrence (ΔAICc = 5.5) compared to the best model for Hypothesis 3. The best model for Hypothesis 4 contained the same variables as for Hypothesis 3, except that the basal area of spruce snags was replaced by the more specific basal area of spruce snags of decay class 3 and a variable for the basal area of dying deciduous trees was included in the model (although the latter was not statistically significant; p=0.050).

The basal area of coniferous or spruce snags – occurring at different levels of thematic resolution across the models corresponding to the four hypotheses – consistently obtained the highest sum of Akaike weights across the four hypotheses (range 0.97-1; Table 3). Spruce snags of decay class 3 was important, as one of the variable with highest AICc in the best model of Hypothesis 4 (sum of AICc weights= 1), whereas all variables depicting spruce snags of more advanced decay were comparatively unimportant (Table 3). The value of mean basal area of freshly dead spruce (i.e. decay class 3) was considerably higher in stands with presence of three-toed woodpecker (2.3±1.8 m²/ha) than in stands without woodpeckers (0.6±0.9 m²/ha) (Table 3). The woodpecker was always absent when the basal area of spruce snags of decay class 3 was < 0.009 m²/ha. The probability of occurrence of the three-toed woodpecker increased as basal area of spruce of decay class 3 increased. A probability of occurrence of 0.5 corresponded to a basal area of freshly dead spruce of 1.8 m²/ha, while a probability of occurrence of 0.9 corresponded to 4.1 m²/ha (Figure 5).

Living deciduous trees were included in all best models and had high sum of AICc weights (0.79-1; Table 3), whereas variables representing living conifers performed relatively

poorly (Table 3). Still, dying pines had a significant positive coefficient in Hypotheses 3 and 4 (Table 2) and the sum of AICc weights of this variable was relatively high (0.53-0.91; Table 3).

Stand area was present in the best models for all four hypotheses and had a significant positive relation to presence of the woodpecker. This variable had a high sum of Akaike weights overall (0.95-1; Table 3). In contrast, local landscape quality was never included in the best model and had a consistently low sum of AICc weights (0.095-0.31; Table 3).

Table 2- Best Generalized Linear Models (binomial errors and logit link) for presence/absence of the three-toed woodpecker for each of the four hypotheses, with values of estimate, standard error and p-value (based on likelihood ratio test).

Best model	**Estimate**	**Standard Error**	**p-value**
Hypothesis 1			
Residual deviance 32.8, AICc 41.9			
BA coniferous snags	0.82	0.28	**<0.001**
Stand Area	0.25	0.10	**0.0025**
BA living deciduous trees	0.86	0.39	**0.013**
Hypothesis 2			
Residual deviance 28.14 , AICc 40.1			
BA spruce snags	1.45	0.48	**<0.001**
Stand Area	0.26	0.11	**0.0029**
BA living deciduous trees	0.91	0.46	**0.019**
Hypothesis 3			
Residual deviance 23.8 , AICc 39.6			
BA spruce snags	1.81	0.61	**<0.001**
BA living deciduous trees	1.34	0.59	**0.0038**
Stand Area	0.32	0.14	**0.0014**
BA dying pines	16.38	8.058	**0.037**
Hypothesis 4			

Residual deviance 19.57, AICc 34.1			
BA spruce snags of decay class 3	2.38	0.81	**<0.001**
Stand Area	0.35	0.15	**<0.001**
BA living deciduous trees	2.27	0.99	**<0.001**
BA dying pines	24.37	11.14	**0.0099**
BA dying deciduous trees	-36.76	21.31	0.050

Legend: BA: Basal area

Table 3- Mean, standard deviation, minimum and maximum for each of the variables included in the global models, with respect to the presence/absence of three-toed woodpecker. The rightmost column presents the sum of AICc weights of each individual variable across all possible models.

	Measured values (n = 40)		**AICc weight**
	Present	**Absent**	
Variables	**Mean ± SD (range)**	**Mean ± SD (range)**	
Hypothesis 1			
BA coniferous snags (m²/ha)	3.85±2.41 (0.85-7.79)	1.93±2.01 (0.13-8.78)	0.97
Stand Area (ha)	11.81±6.85 (4.47-24.56)	8.03±3.84 (3.47-15.00)	0.95
BA living deciduous trees (m²/ha)	2.37±1.61 (0.20-5.18)	2.24±1.51 (0.00-5.19)	0.85
BA deciduous snags (m²/ha)	0.98±0.83 (0.25-3.09)	0.64±0.92 (0.03-4.00)	0.34
Local landscape quality	11.66±5.43 (4.26-25.38)	10.88±7.19 (2.46-27.06)	0.31
BA living conifers (m²/ha)	17.76±7.31 (6.66-36.45)	22.96±10.79 (0.00-51.10)	0.25
Hypothesis 2			
BA spruce snags (m²/ha)	2.45±1.86 (0.38-5.00)	0.72±0.94 (0.03-4.30)	0.99
Stand Area (ha)	11.81±6.85 (4.47-24.56)	8.03±3.84 (3.47-15.00)	0.96
BA living deciduous trees (m²/ha)	2.37±1.61 (0.20-5.18)	2.24±1.51 (0.00-5.19)	0.79
BA living spruces (m²/ha)	8.36±7.30 (0.08-21.62)	11.58±6.39 (0.00-23.54)	0.31
Local landscape quality	11.66±5.43 (4.26-25.38)	10.88±7.19 (2.46-27.06)	0.22
BA pine snags (m²/ha)	1.40±0.82 (0.03-2.94)	1.20±1.50 (0.05-5.33)	0.21
BA deciduous snags (m²/ha)	0.98±0.83 (0.25-3.09)	0.64±0.92 (0.03-4.00)	0.21
BA living pines (m²/ha)	9.40±5.03 (0.72-15.85)	11.38±7.99 (0.00-28.56)	0.19
Hypothesis 3			
BA spruce snags (m²/ha)	2.45±1.86 (0.38-5.00)	0.72±0.94 (0.03-4.30)	1
Stand Area (ha)	11.81±6.85 (4.47-24.56)	8.03±3.84 (3.47-15.00)	0.99
BA living deciduous trees (m²/ha)	2.37±1.61 (0.20-5.18)	2.24±1.51 (0.00-5.19)	0.89
BA dying pines (m²/ha)	0.07±0.08 (0.00-0.24)	0.04±0.08 (0.00-0.40)	0.53
BA living spruces (m²/ha)	8.36±7.30 (0.08-21.62)	11.58±6.39 (0.00-23.54)	0.25
BA dying deciduous trees (m²/ha)	0.03±0.04 (0.00-0.12)	0.05±0.11 (0.00-0.55)	0.19

BA dying spruces (m²/ha)	0.01±0.02 (0.00-0.07)	0.03±0.06 (0.00-0.24)	0.19
BA deciduous snags (m²/ha)	0.98±0.83 (0.25-3.09)	0.64±0.92 (0.03-4.00)	0.17
Local landscape quality	11.66±5.43 (4.26-25.38)	10.88±7.19 (2.46-27.06)	0.16
BA pine snags (m²/ha)	1.40±0.82 (0.03-2.94)	1.20±1.50 (0.05-5.33)	0.15
BA living pines (m²/ha)	9.40±5.03 (0.72-15.85)	11.38±7.99 (0.00-28.56)	0.13
Hypothesis 4			
BA spruce snags of decay class 3 (m²/ha)	2.26±1.8 (0.28-4.8)	0.56±0.86 (0.01-4.25)	1
Stand Area (ha)	11.81±6.85 (4.47-24.56)	8.03±3.84 (3.47-15.00)	1
BA living deciduous trees (m²/ha)	2.37±1.61 (0.20-5.18)	2.24±1.51 (0.00-5.19)	1
BA dying pines (m²/ha)	0.07±0.08 (0.00-0.24)	0.04±0.08 (0.00-0.40)	0.91
BA dying deciduous trees (m²/ha)	0.03±0.04 (0.00-0.12)	0.05±0.11 (0.00-0.55)	0.58
BA pine snags (m²/ha)	1.40±0.82 (0.03-2.94)	1.20±1.50 (0.05-5.33)	0.37
BA dying spruces (m²/ha)	0.01±0.02 (0.00-0.07)	0.03±0.06 (0.00-0.24)	0.24
BA deciduous snags (m²/ha)	0.98±0.83 (0.25-3.09)	0.64±0.92 (0.03-4.00)	0.16
BA living spruces (m²/ha)	8.36±7.30 (0.08-21.62)	11.58±6.39 (0.00-23.54)	0.14
BA spruce snags of decay class 4 with more than 50% of bark (m²/ha)	0.08±0.08 (0.00-0.30)	0.07±0.09 (0.00-0.40)	0.13
BA spruce snags of decay class 5, 6 and 7 (m²/ha)	0.05±0.04 (0.00-0.12)	0.05±0.07 (0.00-0.29)	0.1
BA spruce snags of decay class 4 with less than 50% of bark (m²/ha)	0.06±0.06 (0.00-0.20)	0.05±0.07 (0.00-0.26)	0.098
Local landscape quality	11.66±5.43 (4.26-25.38)	10.88±7.19 (2.46-27.06)	0.095
Basal area of living pines (m²/ha)	9.40±5.03 (0.72-15.85)	11.38±7.99 (0.00-28.56)	0.078
Mean dbh of spruce snags (class 3 to 7) (cm)	15.15±2.48 (12.12-19.63)	14.03±2.84 (8.75-19.64)	0.074

Legend: BA: Basal area

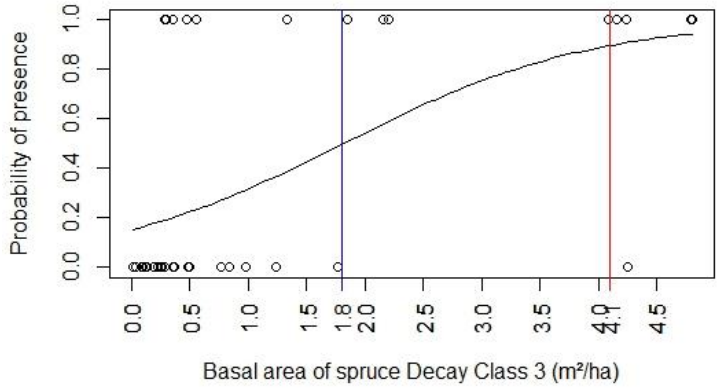


Figure 5- Relationship between the occurrence of three-toed woodpecker and the basal area of spruce of decay class 3. The symbols present the observed amounts for presence and absence and the curve depicts a fitted logistic regression model. This model, with only spruce DC 3 as predictor, has: residual deviance 39.27, p-value < 0.001, AICc 43.6.

4. Discussion

4.1 Determinants of three-toed woodpecker occurrence

My results confirmed each of the four stated hypotheses (see Introduction): gradually increasing the level of thematic resolution of the tree-layer data led to improvements in the statistical model's ability to predict presence of the three-toed woodpecker. I found that the presence of the three-toed woodpecker was related to the abundance of fresh snags, especially recently dead spruce. Spruce has been indicated as a preferred tree species for three-toed woodpeckers (Pechacek and d'Oleire-Oltmanns 2004), and dead and dying spruce with loose bark in particular have been suggested as being important (Kajtoch et al. 2013). In the classification system used in the present study, recently dead spruce belong to decay class 3. This means that the tree is dead, but still has almost all its bark attached. This is of particular importance for three-toed woodpeckers because bark beetles are a key component of their diet. Bark beetles are usually most abundant on spruces (Fayt 2004), and they usually feed upon the cambium of recently dead trees. Siitonen (2001) delineated different successional stages in wood decomposition: the first stage, namely decay class 3 in my study, lasts only a few years after the death of the trees. Bark beetles (subfamily Scolytinae), phloem-feeding weevils (Curculionidae) and longhorn beetles (Cerambycidae) are those that first colonize freshly dead or weakened trees. These insects form the bulk of the three-toed woodpecker´s diet. Therefore the preservation and continuous supply of a proper amount of fresh dead wood is of crucial importance for the persistence of the species.

The attention on dead wood as an indicator of forest naturalness and biodiversity has increased in the last decades, following the decrease in the amount of dead wood in managed boreal forests during the 20th century (Svensson 2013). Both Siitonen (2001) and Östlund (1993) found a reduction in the amount of dead wood of almost 90% during last century in managed forest. Focusing on the northern part of Sweden, different authors have reported dead wood amounts in unmanaged and managed forest. Östlund and Linder (1998) found a mean volume of dead wood of around 11-13 m^3/ha in unmanaged forests, this in contrast to 0.5-1 m^3/ha in managed forests. Fridman and Walheim (2000) found, for managed productive forestland in the Västerbotten county, a volume of 4.1 m^3/ha of logs, and 1.6 m^3/ha for snags. Regarding fresh dead wood, this was underrepresented in comparison to other decay stages in the study by Fridman and Walheim (2000). The volume of freshly dead snags and logs was 1-2 m^3/ha, with a higher presence in forests older than 100 years. Relative volume for the 'slightly decayed' class in logs and snags was less than 15% (Fridman and Walheim 2000).

The amount of dead wood has increased in Sweden during recent years, from 2.1 m^3/ha of hard dead wood in 1996 to almost 4.1 m^3/ha in 2011 (www.miljomal.se).
In the present study I found a threshold of at least 1.8 m^2/ha of spruce snags of decay class 3 for a 0.5 probability of occurrence of the woodpecker. This is higher than what Bütler et al. (2004b) recommend in their study, as they consider a basal area higher than 0.9 m^2/ha as favorable for the woodpecker. I found that for a basal area of spruce snags of decay class 3 of 4.1 m^2/ha, the three-toed woodpecker has a probability of 0.9 to occur. This value is much higher than the 1 m^2/ha that Roberge et al. (2008) found in south-central Sweden. A difference between my study and that of Roberge et al. (2008) is that I focused on measuring dead wood in the area actually used by the woodpeckers. Their study was done at a larger spatial scale where the fixed survey units of 100 ha included some proportion of forest which was probably not used by the woodpecker (e.g. clearcuts, young forest). Hence, by using a finer scale of sampling, my study is more likely to represent truly suitable habitat for the woodpecker.
Czeszczewik et al. (2013) suggest to leave in coniferous reserves at least 2 m^2/ha (basal area) of freshly killed spruce. The value found in the present study for the mean basal area of spruce snags of decay class 3 in stands with presence of the three-toed woodpecker (2.26±1.8 m^2/ha) is in accordance to that (Table 3).

The basal area of spruce snags of decay class 3 found in this study can be converted into wood volume using the following function: Volume = basal area · tree height · shape index (Anon. 1986, Bütler et al. 2004a, Roberge et al. 2008). I assume that the mean height of the snags ranged between 15 and 20 m and that the shape index may range from approx. 0.4 to 0.6 (Anon. 1986). With these assumptions it was possible to obtain a rough estimate of the snag volume. Using these values I found a fresh spruce snag volume of approximately 11-22 m^3/ha for a probability of woodpecker occurrence of 0.5 for the three-toed woodpecker, while for a probability of occurrence of 0.9 the volume of spruce snags would be approximately 25-49 m^3/ha. These values are generally in line with those found in unmanaged boreal forest areas (Östlund and Linder 1998), except for the large amount found for 0.9 of probability of occurrence. Butler et al. (2004a) suggested a volume of at least 15 m^3/ha of snags, which is similar to the value I obtained for 0.5 probability of presence but not to my value for a 0.9 probability. An amount of fresh snags of almost 50 m^3/ha is rare even in unmanaged forests and would mostly occur after some major disturbance such as fire or an insect outbreak. In the case of this study, the stands that had been burned present a large amount of dead wood, in particular of dead spruce, and this could explain why I found this high value.

Living deciduous trees had a positive relation with the occurrence of three-toed

woodpecker. Three-toed woodpecker may forage on deciduous trees, although almost exclusively on dead and sometimes decaying part of living trees (Hogstad 1977). Roberge et al. (2008) argued that deciduous trees may contribute to habitat quality for this species. Moreover, living deciduous species can be important for breeding, as they (especially birch) offer potential nest sites for the species.

The amount of dying pines was positively related to the presence of the woodpecker species in the stands. Although the three-toed woodpecker mainly utilizes spruce (Fayt 1999), it also forages on pine, as the American three-toed woodpecker *Picoides dorsalis* B. does (Crockett and Hansley 1978). In the present study dying pines were most abundant in stands that had been burned. During burnings spruce is often directly killed quickly by fire, while most pines die more gradually over a longer period of time. These stressed pines are in the years after fire more vulnerable to bark beetle attacks and can provide food to the woodpecker for a longer period of time after fire that instantaneously killed trees. This can explain why this variable was found important in the last (and overall best) model.

Bütler et al. (2004a) investigated the occurrence of the three-toed woodpecker in Switzerland and Sweden related to the amount of both snags and logs (i.e. lying dead trees), finding a positive relationship in both cases. Also Roberge (2008) found a significant relationship between the presence of the woodpecker and the amount of lying dead wood, while Wesołowski et al. (2005) remarked the importance of standing and downed dead spruces for the occurrence of the species. In the present study logs have not been taken in consideration in spite of the fact that the three-toed woodpecker may also occasionally forage on lying dead trees (Bütler et al. 2004a). On the other hand, the apparent relation between the woodpecker and the amount of lying dead wood observed in other studies could be due to the higher abundance of lying dead trees in forests with more snags. Therefore, there is a need for further studies evaluating whether lying dead wood has a direct mechanistic influence on habitat quality for the three-toed woodpecker.

Stand size was positively related with the presence of three-toed woodpecker. This confirms the results of Imbeau and Desrochers (2002), who observed that the occurrence of the closely-related American three-toed woodpeckers was strongly related with the area of suitable habitat around their playback stations. Other studies on old-growth forest bird species support that there is a positive effect of the area on the occurrence of birds (Virkkala et al. 1994, Edenius and Elmberg 1996, Brotons et al. 2003). Stand size may have ecological importance, but it may also have an influence through pure sampling effects. If we consider that the woodpeckers' home ranges may stretch outside the study stands, then the probability of encountering a woodpecker in a stand is theoretically higher in larger

stand compared to smaller stands, because my woodpecker survey covered the whole area of each stand. To explore the possibility that the probability to encounter a three-toed woodpecker was higher in larger stands due to random sampling effects, I fitted a GLM (Poisson distribution) where the explanatory variable was stand area and the response was the number of visits with detection of the three-toed woodpecker within the study stand. I included only the stands where at least one woodpecker was detected during the survey season. The rationale is that if the positive effect of stand area on woodpecker presence is a simple sampling artifact, then (in sites with presence of the woodpecker) the number of visits where woodpecker was present should theoretically increase with an increase in stand size. I found that there was no significant relationship ($p= 0.23$) between stand area and the number of visits with woodpecker presence. This suggests that random sampling is not the main driver underlying the positive relationship between stand area and three-toed woodpecker occurrence. Instead, this relationship can be due to the differences in resource availability. It is expected that the amount of resources for the woodpecker probably increases with increasing stand area, as most of my study stands were surrounded by less suitable types of forest, clearcuts or wetlands.

The variable representing local landscape quality (percentage of old forest within 1 km) did not contribute significantly to predicting the occurrence of three-toed woodpecker. The home-range size of the three-toed woodpecker has been estimated to be between 100-400 ha (Pechacek 2004), and it approximately corresponds at a radius of 1 km. However, such a radius may be not large enough to detect a landscape effect. Moreover, the landscape variable I used (i.e. the percentage of old forests in the surroundings) may not be a good proxy for landscape quality. It is known that forest fragmentation and the amount of edges can be good predictors for occurrence of forest specialists bird species (Jokimaki and Huhta 1996). Thus, a lot of small patches of old forest may be less suitable to the three-toed woodpecker than a large patch of continuous forest. I did not consider habitat fragmentation as such in this analysis, and it could be an explanation of why this variable did not show significance in the models. In addition, the kNN data is based on satellite data and hence it has limitations when it comes to estimating forest age. This may have influenced the quality of my landscape variable.

4.2 Management implications

My results support previous findings that three-toed woodpecker requires large forest patches with high densities of dead spruce (Amcoff and Eriksson 1996). In addition, I have refined the knowledge about the species' habitat requirements and found that dead wood quality can be more important in predicting the occurrence of the three-toed woodpecker

than coarser measures of total 'dead wood' or snag amounts. Indeed, this study has not only confirmed the importance of dead wood for the three-toed woodpecker, but has delineated which type of dead wood is most important for explaining the occurrence of this bird during the breeding season. Based on my results I would suggest improving specific management targets for the three-toed woodpecker. It was shown that coniferous snags are an important predictor for three-toed woodpecker presence; nevertheless I have shown that accounting for tree species and decay classes can further improve the habitat models. Dead wood quality should therefore be taken into consideration for the management of the species.

To ensure the persistence of the species, and to guarantee a high quality habitat for specialized woodpeckers, it will be necessary to implement new forest management practices. To maintain and enhance biodiversity in managed forests it has been suggested to leave all dead trees and some living trees during logging operation, or to kill some living trees to create dead wood (Esseen et al. 1992). Important actions, as reported by Jonsson et al. (2005), are: increasing the protection of remaining semi-natural forests with abundant dead wood; creating dead wood during thinning operations; prolonging rotation times in mature stands rich in dead wood; and increasing connectivity among suitable habitats. Moreover, some restoration actions such as prescribed burning may provide an effective way to provide suitable habitat for the three-toed woodpecker. Interestingly, 7 of the 14 stands with presence of the woodpecker in the present study were prescribed burnings (which represented 10 of the 40 stands). In comparison, gap cuttings were not as strongly represented among stands with presence of the woodpecker (Appendix 1). When implementing conservation measures involving the creation of fresh dead wood, it will be important to ensure a continuous supply of that substrate over time, for example by ensuring that a some proportion of the forest in a given landscape is burned every 10 years or so.
Ensuring the right habitat for three-toed woodpecker may also benefit several other species. Indeed, Mikusiński et al. (2001) and Roberge and Angelstam (2006) found that the presence of this specialized woodpecker was the best predictor of forest bird diversity and species richness of forest specialists.

Future challenges will be the maintaining of a viable population of three-toed woodpecker, as one of the main concern is the possibility that the Swedish population is already below the threshold level for the woodpecker population capacity (Hanski and Ovaskainen 2000). Additional studies on the requirements of three-toed woodpecker in the boreal region could refine the knowledge about features of the species' habitat, in a perspective of preserving the population. More precisely, it would be interesting to investigate the effects of different

restoration actions on habitat quality of three-toed woodpecker and how recently adopted conservation measures in forestry (e.g. tree retention at harvesting, dead wood creation, set-aside establishment) could lead to improvements in the species' population status.

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Appendix 1

Appendix 1- Number of sightings and index of presence/absence (see before) per each stand, with the management history

Stand number	Management history	Number of forest vegetation plots used in the analyses	Number of visits with sighting of the woodpecker	TTW Breeding index
3	Gap cutting	3	0	0
4	Gap cutting	6	0	0
5	Unmanaged control set-aside	3	0	0
10	Gap cutting	5	0	0
12	Unmanaged control set-aside	4	0	0
13	Burning	3	0	0
14	Unmanaged control set-aside	3	0	0
16	Gap cutting	9	0	0
18	Gap cutting	2	0	0
19	Unmanaged control set-aside	2	0	0
21	Burning	5	0	0
22	Burning	5	0	0
23	Unmanaged control set-aside	8	0	0
25	Gap cutting	2	0	0
31	Nature reserve	6	0	0
32	Nature reserve	6	0	0
34	Nature reserve	7	0	0

36	Nature reserve	10	0	0
38	Nature reserve	6	0	0
1	Gap cutting	10	1	0
15	Gap cutting	4	1	0
17	Unmanaged control set-aside	3	1	0
24	Unmanaged control set-aside	5	1	0
26	Unmanaged control set-aside	3	1	0
35	Nature reserve	5	1	0
39	Nature reserve	4	1	0
8	Burning	4	2	1
9	Gap cutting	3	2	1
11	Gap cutting	8	2	1
30	Nature reserve	6	2	1
37	Burning	3	2	1
20	Unmanaged control set-aside	6	3	1
28	Burning	6	3	1
40	Nature reserve	4	3	1
7	Unmanaged control set-aside	14	4	1
29	Burning	16	4	1
33	Nature reserve	14	4	1
6	Burning	3	5	1

27	Burning	11	5	1
2	Burning	5	6	1

SENASTE UTGIVNA NUMMER

2015:7 The impact of abiotic factors on daily spawning migration of Atlantic salmon (Salmo salar) in two north Swedish rivers
Författare: Anton Holmsten

2015:8 Restoration of white-backed woodpecker *Dendrocopos leucotos* habitats in central Sweden – Modelling future habitat suitability and biodiversity indicators
Författare: Niklas Trogen

2015:9 BEYOND GENOTYPE Using SNPs for pedigree reconstruction-based population estimates and genetic characterization of two Swedish brown bear (Ursus arctos) populations
Författare: Robert Spitzer

2015:10 Hot, hungry, or dead: how herbivores select microhabitats based on the trade-off between temperature and predation risk
Författare: Kristina Vallance

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Författare: Sebastian Olofsson

2015:12 Evaluating lake charr (*Salvelinus namaycush)* temperature use in a mountain lake using acoustic telemetry
Författare: Johan Leander

2015:13 Hormonbehandlade mårdhundstikar – En framtida förvaltningsmetod för att förhindra en storskalig etablering av mårdhund i Sverige?
Författare: Erika Bergmark

2015:14 Hunting dogs in Sweden: Are the abundances of hunting dog breeds influenced by the population sizes of game species?
Författare: Linnea Aronsson

2015:15 The effect of migratory fish on freshwater ecosystem nutrient dynamics
Författare: Magnus Enbom

2015:16 Restoration of natural disturbances: impact on distribution and performance of dominant ants (*Formica spp.*) by fire and gap dynamics
Författare: Rebecca Larsson

2015:17 Life History Trade-offs in Anadromous Burbot Lota Lota (*Linnaeus 1758*) from Rickleån and Sävarån, Northern Sweden
Författare: Mikael Sandberg

2015:18 Laxens uppströmsvandring i den restaurerade och flödesreglerande Umeälvens nedre del
Författare: Joakim Johansson

2016:1 Moose (Alces alces) browsing patterns in recently planted clear-cut areas in relation to predation risk of the gray wolf (Canis lupus) in Sweden
Författare: Suzanne van Beeck Calkoen